

Family Desmoxyidae Hallmann, 1917

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Desmoxyidae Hallmann (Demospongiae, Halichondrida) contains 19 genera, 10 of which are recognised here, and probably less than 100 species worldwide. Desmoxyids are widely distributed and live mainly in shallow coastal waters but a few have also been recorded from 1300 m depth. Major morphological characters diagnostic for the family include spined or smooth diactinal microscleres (oxeas or strongyles), often centrangulate or strongly bent centrally, localised in the ectosomal region; choanosomal skeleton with monactinal (styles or tylostyles) and/or diactinal spicules forming confused reticulate tracts or widely spaced, irregular multispicular bundles bound together by sparse collagen, or enclosed in poorly developed fibres; microscleres also sometimes include raphides occurring singly or in bundles (trichodragmata), or acanthose microrhabds (sanidaster-like), acanthose cladotoxa and birotules.

Keywords: Porifera; Demospongiae; Halichondrida; Desmoxyidae; *Acanthoclada*; *Didiscus*; *Halicnemia*; *Heteroxya*; *Higginsia*; *Julavis*; *Microxistyla*; *Myrmekioderma*; *Negombo*; *Parahigginsia*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Heteroxyinae Dendy, 1905 (*nomen oblitum*). Desmoxyinae Hallmann, 1917c. Desmoxyidae Bergquist, 1970. Higginsinae de Laubenfels, 1936a.

Definition

Halichondrida with smooth or spined, usually centrangulate microxea microscleres or modified forms forming an ectosomal skeleton.

Diagnosis

Encrusting, massive or ramose sponges often with hispid or conulose surfaces bearing smooth or spined microxea microscleres, often centrangulate or strongly bent centrally, sometimes acanthose and rhabdose, usually found localised on the ectosome, sometimes also with raphides occurring singly or in bundles (trichodragmata), or acanthose cladotoxa and birotules in one genus; megascleres monactinal (styles or tylostyles), diactinal (oxeas, strongyles) or both; choanosomal skeleton a confused arrangement of single spicules or widely spaced reticulate bundles of multispicular fibres, with little spongin, with poorly developed or no axial compression, and a relatively poorly differentiated extra-axial skeleton (disorganised-plumose).

Scope

Of 19 nominal genera only 10 are considered to be valid and presently included in Desmoxyidae.

History and biology

The family was established initially for five genera, of which only three were correctly assigned (*Desmoxya*, *Higginsia* and *Halicnemia*). Many other genera were subsequently added or associated with the family by various authors, although affinities between

them were not always completely clear. Topsent (1928c) subsequently removed most of these spurious genera to Hemiasterellidae, but Wiedenmayer (1977b) suggested that although some were hemiasterellids, others were more appropriately included in Hadromerida (e.g., *Paratimea* Hallmann) or Astrophorida (e.g., *Holoxea* Topsent, 1892a). Hooper & Lévi (1993b) discuss the affinities of other genera included in Desmoxyidae at one time or another.

Several desmoxyid genera have received recent attention in isolation, although prior to the present work there has been no comprehensive synthesis or revision of the entire family. Contemporary reviews include: Bergquist (1965) and Hooper & Lévi (1993b) for *Myrmekioderma* and *Higginsia*; Van Soest *et al.* (1990), Hiemstra & Van Soest (1991) and Diaz *et al.* (1993) for *Myrmekioderma* and *Didiscus*; Pansini & Pesce (1998) for *Higginsia*; and Van Soest & Lehnert (1997) for *Julavis*, also providing the most recent overview of the family.

Together these reviews have moved closer towards a more homogeneous definition and scope of Desmoxyidae, although there is still controversy as to the true affinities of *Myrmekioderma* and *Didiscus*.

Bergquist (1965) provides a good historical overview on the chequered history of taxonomic placement of *Myrmekioderma*, including: subfamily Heteroxyinae (Dendy, 1905) in the family Haploscleridae; section Heteroxyeae, subfamily Axinellidae, family Desmacidonidae (Dendy, 1922b); family Jaspidae, order Epipolasida (Wilson, 1925); family Heteroxyidae (Topsent, 1928c); family Phorbasidae (de Laubenfels, 1936a); section Raspelieae, family Axinellidae (Burton, 1937).

Of contemporary authors, Hooper & Lévi (1993b) included *Myrmekioderma* in Desmoxyidae, following Bergquist (1965), based on its morphological similarities with *Higginsia* (e.g., spined ectosomal spicules), with empirical support from chemotaxonomic studies of both genera and outgroups. Conversely, Van Soest *et al.* (1990), Hiemstra & Van Soest (1991) and Diaz *et al.* (1993) referred *Myrmekioderma* to Halichondriidae based on the halichondroid nature of its more-or-less confused choanosomal skeleton, possession of a detachable ectosomal crust, and the fact that the acanthose nature of the ectosomal spicules was not as prominent for the genus as previous authors had indicated. *Didiscus* was also included in the Halichondriidae based on its very close morphological resemblance

to *Myrmekioderma* (external features, skeletal architecture). However, Van Soest & Lehnert (1997) subsequently agreed that both *Myrmekioderma* and *Didiscus* should be returned to the Desmoxyidae, indicating further that *Julavis* represented a close link between *Higginsia* and *Myrmekioderma*, possessing both coarsely spined diactinal surface spicules (like *Higginsia*) and wispy trichodragmata (like *Myrmekioderma*).

Of other genera, Hooper & Lévi (1993b) retained *Holoxea* Topsent in the Desmoxyidae following Hallmann (1917c), which had sanidaster-like microxeas associated with the ectosome, in addition to raphides in trichodragmata. However, re-examination of the type species (*H. furtiva* Topsent, 1892a; MNHN DT2414) confirms that these are not true microxeas but more similar to the spiny microrhabds seen in *Meloplus* Thiele, and the genus is more appropriately referred to Ancorinidae (Astrophorida) (see chapter by Uriz, this volume).

Differences with similar families

Although Topsent (1928c) implied close affinities between desmoxyids and hemiasterellids, more recent concepts of the family (e.g., Hooper, 1986; Voultsiadou-Koukoura & Van Soest, 1991a) restrict the latter to forms with asterose microscleres (in Hadromerida), whereas desmoxyids have only microxeote

spicules, and closer affinities to other halichondrids. On that basis it could also be argued that several genera currently assigned to Bubaridae (e.g., *Cerbaris* and junior synonyms *Rhabdoploca*, *Bubaropsis*) also have inferred affinities with the Desmoxyidae, having acanthose or smooth oxete megascleres, but these also have quite different skeletal structures and megasclere geometries (non-actinal spicules with heads embedded in a basal layer of interlacing vermiform diactinal spicules). The presence of smooth or spined oxeads, generally associated with the ectosomal skeleton, is characteristic of, and apomorphic for, desmoxyid genera. These spicules are traditionally classed as microscleres (e.g., Hallmann, 1917c; Wiedenmayer, 1977b), although in comparison to many other taxa they are generally much too large to be considered as such.

Negombo Dendy is transferred to Desmoxyidae in this work following Kelly (pers. comm.), with suspected affinities to *Didiscus*, although this relationship is not completely clear and requires further corroboratory evidence from other sources (e.g., molecular data).

Previous reviews

Bergquist (1965), Wiedenmayer (1977b), Van Soest *et al.* (1990), Hiemstra & Van Soest (1991), Diaz *et al.* (1993), Hooper & Lévi (1993b), Van Soest & Lehnert (1997), Pansini & Pesce (1998).

KEY TO GENERA

- | | |
|--|----------------------|
| (1) Microscleres (acantho-)microxeas | 2 |
| Microscleres discorhabd-like microxeas | <i>Didiscus</i> |
| Microscleres sanidaster-like acanthose microrhabds | <i>Negombo</i> |
| Microscleres raphides | 4 |
| Microscleres acanthose cladotoxas and birotules | <i>Acanthoclada</i> |
| Microscleres absent | <i>Heteroxya</i> |
| (2) Cortex absent, without microscleres or with microscleres scattered but not confined to the surface | <i>Higginsia</i> |
| Cortex moderate with scattered microscleres concentrated near surface | <i>Parahigginsia</i> |
| Cortex well-developed, with an erect palisade of microscleres perpendicular to the surface | 3 |
| (3) Extra-axial megascleres centrangulate oxeads | <i>Halicnemis</i> |
| Extra-axial megascleres absent | <i>Microxistyla</i> |
| (4) Ectosomal megascleres acanthose oxeads | <i>Myrmekioderma</i> |
| Ectosomal megascleres raphidiform oxeads | <i>Higginsia</i> |
| Ectosomal megascleres (acantho-)strongyles | <i>Julavis</i> |

ACANTHOCLADA BERGQUIST, 1970

Synonymy

Acanthoclada Bergquist, 1970: 22.

Type species

Acanthoclada prostrata Bergquist, 1970 (by monotypy).

Definition

Desmoxyidae with a plumose or hymedesmioid basal skeleton composed of rhabdostyles and bases of choanosomal styles perpendicular to the substrate; choanosomal skeleton lax, composed of ascending tracts of long smooth styles extending into the periphery, terminating in brushes of long centrangulate oxeads; microscleres acanthose cladotoxas and birotules forming a dense ectosomal cortex.

Diagnosis

Thickly encrusting; choanosomal skeleton lax, fibrous, consisting of ascending fibres and tracts reinforced with small quantities of collagen, without distinctive axis; basal skeleton composed of tangled bundles of spicules containing rhabdostyles in plumose or hymedesmioid tracts erect on the substrate bases of larger choanosomal styles embedded in these bundles, and abundant microscleres lying on basal spongin; ascending fibres cored by smooth styles forming multispicular tracts, with smooth rhabdostyles scattered within and protruding from fibres. Long styles also protrude through fibres and abundant microscleres are scattered throughout the mesohyl producing a lax halichondroid skeleton. Subectosomal fibres terminate in brushes of long centrangulate oxeads which form conulose surface projections. Ectosome is also packed with acanthose microscleres. Megascleres include smooth styles, rhabdostyles and oxeads which are usually centrangulate or toxiform. Microscleres acanthose cladotoxas and birotules.

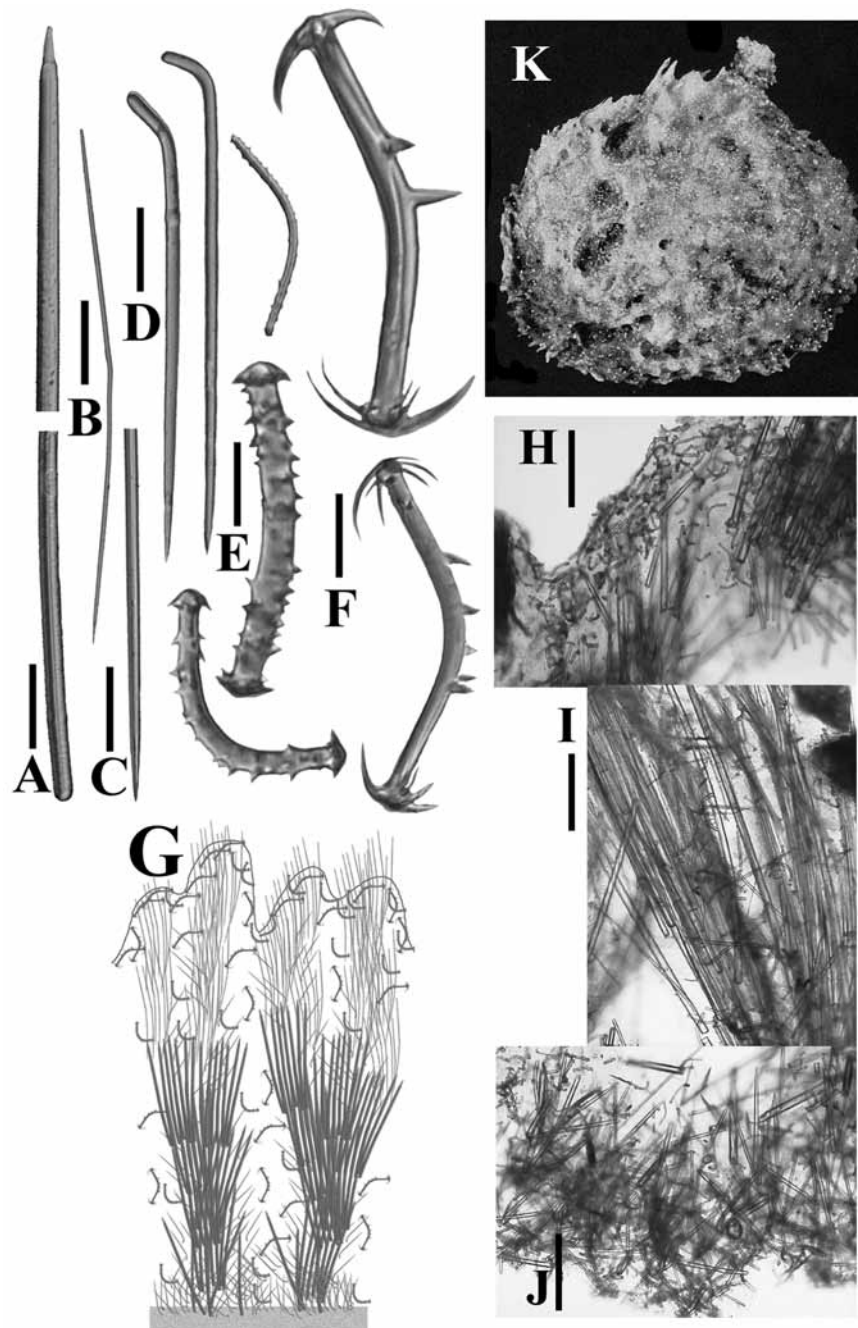


Fig. 1. *Acanthoclada prostrata* Bergquist (holotype). A, base and point of choanosomal style (scale 100 μm). B, centrangulate oxea (scale 200 μm). C, enlarged apex of oxea (scale 100 μm). D, rhabdostyles (scale 50 μm). E, birotules (scale 15 μm). F, cladotoxas (scale 15 μm). G, idealised reconstruction of skeleton. H, ectosomal skeleton (scale 200 μm). I, subectosomal skeletal tracts (scale 200 μm). J, basal skeleton (scale 200 μm). K, holotype (from Bergquist, 1970: pl. 5B).

Description of type species

Acanthoclada prostrata Bergquist, 1970 (Fig. 1).

Synonymy. *Acanthoclada prostrata* Bergquist, 1970: 22.

Material examined. Holotype: NMNZ Por.27 – Takatu Point, New Zealand.

Description. Thick, slimy, encrusting on a bivalve, firm texture, granular surface raised into conules; ectosomal skeleton consists of bundles of centrangulate oxeas ($960\text{--}1320 \times 1\text{--}9 \mu\text{m}$) embedded in the ends of choanosomal skeletal tracts, protruding through the surface in erect bundles (mainly at the ends of surface

conules) or forming paratangential tracts near the surface, and the surface is also densely packed with spined birotule-like microscleres ($52\text{--}72 \times 3\text{--}4 \mu\text{m}$) and ‘cladotoxas’ ($80\text{--}96 \times 5\text{--}6 \mu\text{m}$); choanosomal skeleton with two more-or-less distinct components: basal skeleton consists of entirely smooth rhabdostyles with a prominent basal rhabd ($213\text{--}600 \times 6\text{--}8 \mu\text{m}$) forming dense plumose or hymedesmioid bundles erect on the the substrate, and also with the bases of choanosomal styles embedded, usually in bundles, within this tangled basal spicular network and standing perpendicular to the substrate; ascending component of skeleton consists of thick, more-or-less discrete multispicular tracts coring

light spongin fibres composed of long straight or slightly curved styles with evenly rounded, slightly subtylote, or occasionally subterminal tylote swellings ($677\text{--}1850 \times 9\text{--}18 \mu\text{m}$) standing perpendicular to the substrate and ascending to, but not protruding through the surface; longer, more curved styles also project out from skeletal tracts and tracts are also sparsely 'echinated' with rhabdostyles (although the latter are mostly concentrated at the base of the skeleton); mesohyl also contains individual styles, bundles of oxeas erect or running transversely through the skeleton, and abundant microscleres are scattered throughout the skeleton together producing a lax halichondroid skeletal structure.

Remarks. Bergquist (1970) assigned *Acanthoclada* to Desmoxyidae because the overall skeletal pattern was similar to *Higginsia* (lax and lacking any axial compression), differing from the latter in having echinating rhabdostyles and a special category of microscleres termed 'cladotoxas' (curved rhabds with large terminal clads and mostly smooth shafts, or with few larger hook-like spines at the centre) somewhat resembling the cladotylotes of *Acarinus* (Acarinidae, Poecilosclerida), and 'birotules' (of similar shape but with evenly spined shaft and small terminal hooks). These microscleres appear to be unique amongst the demosponges and as such they are of uncertain derivation and affinity within Desmoxyidae. Unlike the cladotylotes of *Acarinus*, which comprise a special category of megasclere, these cladotoxas in *Acanthoclada* are much smaller relative to its style and oxea megascleres and clearly represent a special category of microsclere (and thus the affinities between these two genera appear to be merely superficial). Bergquist (1970) recorded that rhabdostyles were 'echinating', but this may be a slightly misleading comparison with raspailiids and microcionids. Certainly in the basal part of the skeleton rhabdostyles form plumose or hymedesmioid brushes erect on ('echinating') the surface, whereas they do not appear to 'echinate' the ascending choanosomal spicule tracts but appear to be scattered, embedded or protrude from these tracts at all angles and directions. Consequently, the term 'echinating' is not used in this context.

This genus is somewhat enigmatic within Desmoxyidae (and indeed Halichondrida). Microsclere morphology and derivation is not typical of other desmoxyids, although the birotules are vaguely rhabd-like and are conceivably derived from the rhabd-like microxeas typical of the family. The possession of rhabdostyles is also unusual amongst halichondrids. Morphologically these spicules are very similar to those rhabdose genera of Raspailiidae (*Aulospongia*, *Raspailia* (*Raspaxilla*)), although the two groups have few other affinities. The genus is retained in Desmoxyidae, following Bergquist (1970), being most similar to *Higginsia* based largely on their affinities in skeletal structure, whereas this assignment is still not certain.

Distribution

Monotypic, and known only from New Zealand waters.

DIDISCUS DENDY, 1922

Synonymy

Didiscus Dendy, 1922b: 135; Van Soest *et al.*, 1990: 33; Hiemstra & Van Soest, 1991: 45; Diaz *et al.*, 1993: 145.

Type species

Didiscus placospongioides Dendy, 1922b (by monotypy).

Definition

Desmoxyidae with ectosomal crust of 'discorhabd'-like microxea microscleres.

Diagnosis

Massive-amorphous to lobate growth forms; spicules strewn in confusion and sporadically grouped in spongin-reinforced directionless tracts; ectosomal skeleton is a gradation from a perpendicular palisade to a tangential or paratangential arrangement of spicules with 'discorhabd'-like microscleres arranged perpendicular to the surface; surface with sculptured grooves and subdermal drainage canals.

Description of type species

Didiscus placospongioides Dendy, 1922b (Fig. 2).

Synonymy. *Didiscus placospongioides* Dendy, 1922b: 135.

Material examined. Holotype: BMNH 1921.11.7.112 – Cargados Carajos, W Indian Ocean.

Description. Massively encrusting growth form; surface strongly grooved with angular striations forming polygonal plates; plates contractile with oscula in between; ectosomal skeleton a thick tough crust composed of generally smaller oxeas forming discrete bundles in a continuous palisade, erect, paratangential or tangential to the surface; discorhabd microscleres generally arranged perpendicular to the surface, and concentrated near the surface singly or in thick tracts; choanosomal skeleton with confused radial tracts of generally larger oxeas, the largest at the centre running mainly longitudinally, with medium and smaller sized oxeas becoming increasingly transverse, eventually carrying the ectosomal crust; spongin moderately developed; megascleres are oxeas more-or-less in two size categories, the smaller sometimes centrotylote, and occasionally with tylote modifications ($400\text{--}1400 \times 11\text{--}20 \mu\text{m}$); microscleres rugose or finely spined microxeas, sharply pointed with 'frayed' or ragged points, possessing two unequally sized discs asymmetrically aligned along the shaft, superficially resembling discorhabds of the Latrunculiidae ($70\text{--}90 \times 2\text{--}5 \mu\text{m}$).

Remarks. There is little doubt that *Didiscus* and *Myrmekioderma* are closely related and belong to the same family, despite the former previously being included with the Hadromerida. Part of the confusion regarding the family placement of *Didiscus* centred on the origin and nature of the discorhabd microxeas, which up until the review of Van Soest *et al.* (1990) were considered to be homologous with the true discorhabds of the latrunculids (formerly Hadromerida, now Poecilosclerida). These authors correctly noted that the lateral disks on microxeas of *Didiscus* were merely highly modified and exaggerated spines on centrotylote microxeas, not related to the streptaster/spiraster origin of true discorhabds. In those examples of microxeas that lacked lateral disks, or where they were rudimentary, there are clear similarities to those of *Myrmekioderma*, with tapering points, granular spination and slightly centrangulated at their centres (Fig. 2C).

Further clues on its affinities can be seen in skeletal architecture, in which both genera have an ectosomal skeleton where smaller oxeas are arranged tangentially, paratangentially or in erect brushes (discorhabd-like microxeas and smaller oxeas in *Didiscus*; smaller oxeas in *Myrmekioderma*). This surface crust is carried by

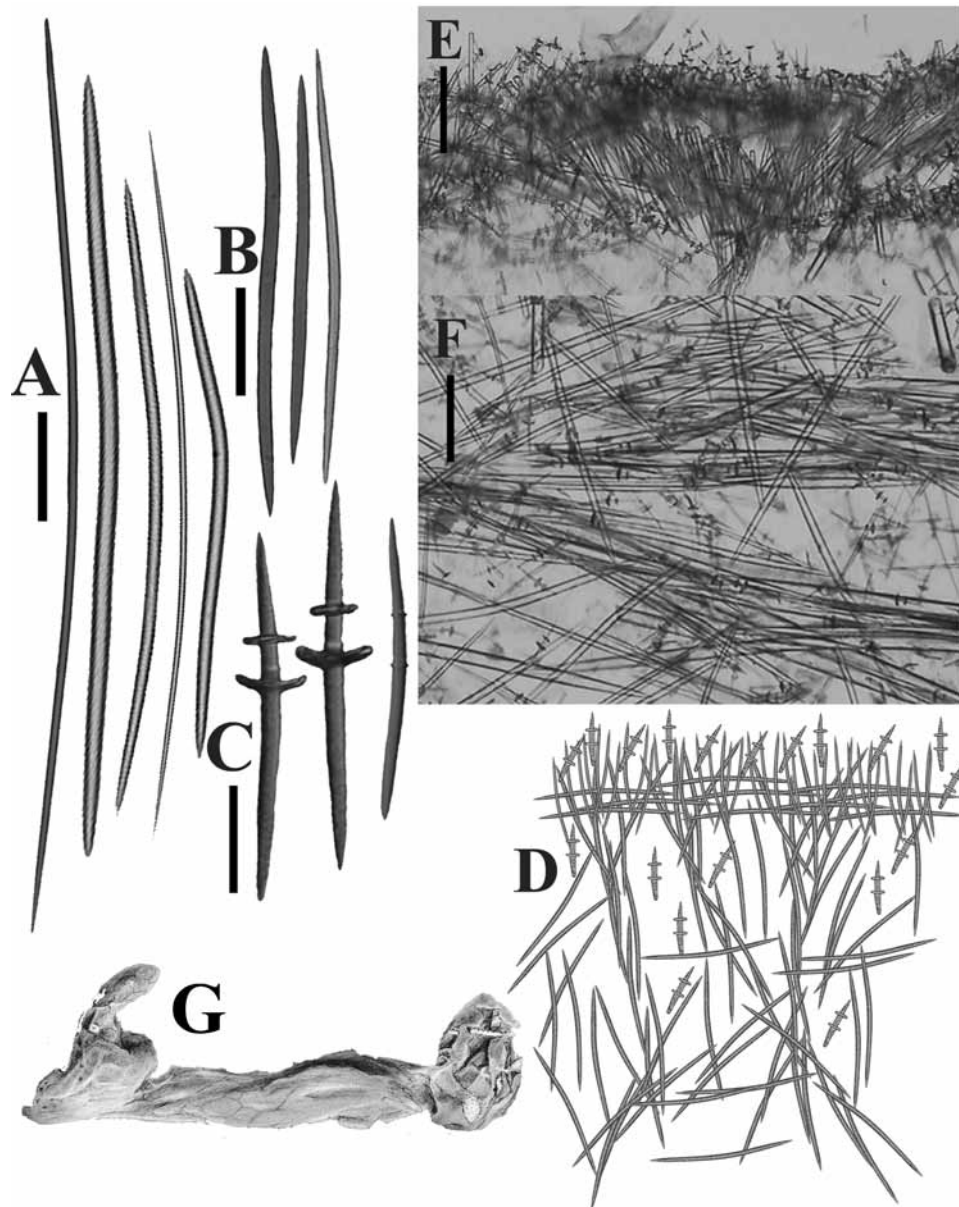


Fig. 2. *Didiscus placospongioides* Dendy (holotype). A, larger oxeas (scale 150 µm). B, smaller oxeas (scale 100 µm). C, discorhabds (scale 25 µm). D, idealised reconstruction of skeleton. E, ectosomal skeleton (scale 200 µm). F, choanosomal skeleton (scale 200 µm). G, holotype (from Dendy, 1922b: pl. 5 fig. 10).

irregular radiating tracts of larger spicules in both genera (Hiemstra & Van Soest, 1991). Diaz *et al.* (1993) further remarked on the similarities between the two genera, citing examples of two Caribbean species, *Didiscus oxeata* and *Myrmekioderma styx*, in which external sculpturing of the surface and skeletal structure were so similar that they were indistinguishable in the field without subsequent microscopic examination. Consequently, *Didiscus* differs substantially only from *Myrmekioderma* in possessing discorhabd-like microxeas and lacking trichodragmata. *Didiscus* and *Myrmekioderma* also consistently produce the same marine natural products chemistry (M.K. Harper, pers. comm.).

Distribution

Tropical, subtropical; Brazil, Caribbean, Mediterranean, NE Atlantic, W Indian Ocean, Indonesia.

HALICNEMIA BOWERBANK, 1864

Synonymy

Halicnemia Bowerbank, 1864: 184, 1866: 96; Topsent, 1897b: 235; Hallmann, 1917c: 675; Topsent, 1928c: 39 (in part); Descatoire, 1966: 239; Van Soest, 1987b: 24; Desqueyroux-Faúndez & Van Soest, 1997: 429. *Alloscleria* Topsent, 1927: 6; 1928c: 160. *Quindesmia* de Laubenfels, 1950. (Taxonomic decision for synonymy: Hooper, this work.)

Type species

Halicnemia patera Bowerbank, 1864: 184 (by monotypy).

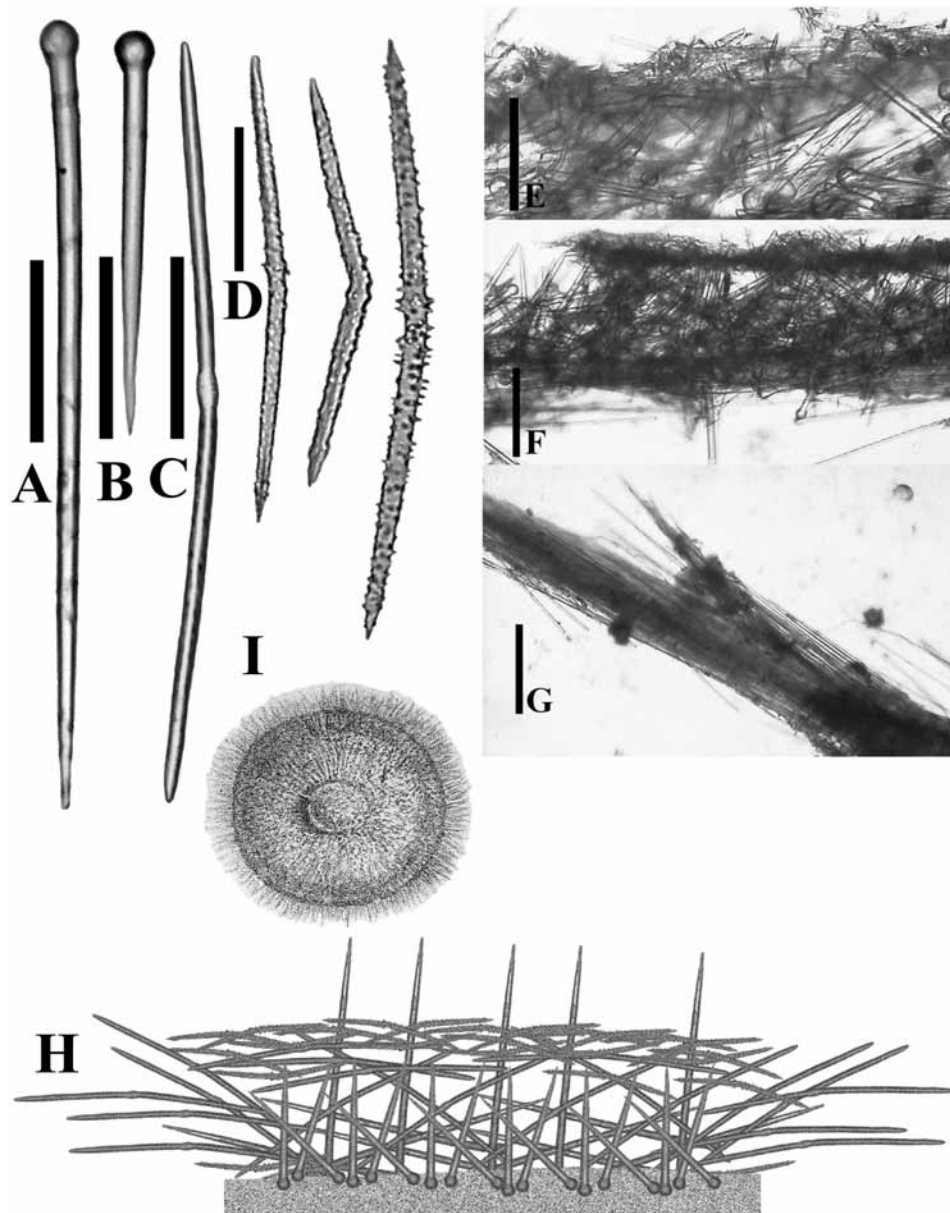


Fig. 3. *Halicnemisia patera* Bowerbank (syntypes). A, larger tylostyle (scale 400 μm). B, smaller tylostyle (scale 200 μm). C, centrotylote oxea (scale 400 μm). D, acanthoxeas (scale 50 μm). E, peripheral skeleton (scale 100 μm). F, choanosomal skeleton (scale 250 μm). G, spicule fringe around margin of disk (scale 250 μm). H, idealised reconstruction of skeleton. I, syntype (from Bowerbank, 1874b: pl. 15 fig. 31).

Definition

Desmoxyidae with acanthose centrangulate microxeas forming erect ectosomal brushes.

Diagnosis

Encrusting or disk-shaped growth forms; surface smooth or minutely conulose and usually very hispid; choanosome reduced to a compressed basal layer of paratangential tracts on the substrate including a halichondroid reticulation of styles with or without polytylote smooth oxeas; styles/tylostyles embedded and erect on the basal layer, protruding through and tangential to the surface; specialised ectosomal spicules consist of erect brushes of acanthose, centrangulate or straight microxeas (best developed in the

type species) and protruding choanosomal megascleres; megascleres of one or two categories, styles/tylostyles with or without polytylote smooth oxeas; microscleres are centrangulate spined microxeas, usually with abrupt angular central curve, sometimes straight.

Description of type species

Halicnemisia patera Bowerbank, 1862b (Fig. 3).

Synonymy. *Halicnemisia patera* Bowerbank, 1862b, pl. 10, pl. 32; 1864: 184; 1874b, pl. 15. *Crella inflata* Arndt, 1935: 76. *Bubaris gallica* Topsent, 1893c: 35.

Material examined. Syntypes: BMNH 1910.1.1.2459–60, 1930.7.3.25 – Shetland Is, N Atlantic.

Description. Thinly encrusting; surface conulose, fibrous, with margins prominently hispid and shaggy from protruding

longer tylostyle megascleres; choanosomal skeleton a basal layer of scattered tylostyles arranged paratangential to the substrate, long centrotylote oxeas forming dense bundles ascending to surface, and a dense mass of small acanthoxeas forming a crust on the surface and subectosomal skeletons; ectosomal skeletons with paratangential crust of microxeas and longer tylostyles protruding through the surface; megascleres include a long tylostyles with a pronounced basal swelling and constriction, entirely smooth, fusiform points ($1400\text{--}2750 \times 35\text{--}55 \mu\text{m}$), smaller tylostyles of similar morphology ($255\text{--}790 \times 15\text{--}32 \mu\text{m}$), and long, thin, centrally bent and centrotylote oxeas ($1200\text{--}1750 \times 10\text{--}15 \mu\text{m}$); microscleres are acanthoxeas with centrotylote swelling, straight or with a central bend, spines range from vestigial to prominent, mostly erect ($125\text{--}215 \times 6\text{--}12 \mu\text{m}$).

Remarks. There is some confusion surrounding the genus *Halicnemia*, arising from Topsent's (1928c: 39) revision of species. Topsent included a diverse assemblage of taxa, including hadromerids, hemiasterellids and true desmoxyids into the genus. Aster-bearing species (e.g., *Bubaris constellata* Topsent), and those with acanthose or smooth microxeas (e.g., *H. patera* Bowerbank, *H. gallica* (Topsent)). *Halicnemia* (*sensu* Topsent) do not form a natural assemblage of taxa, contrary to his (1928c: 39) strong opinions otherwise, although the presence of certain shared characters seems to cut across systematic boundaries (e.g., possession of microxea microscleres). Nevertheless, aster-bearing species are referred to *Stelligera* Gray (family Hemiasterellidae; e.g., Hooper, 1986), those with asters and microxea are probably hadromerids (e.g., *Diplastrella*, *Spirastrella*), whereas *Halicnemia* has only acanthose ectosomal microxeas, very similar in geometry to those seen in *Higginsia*.

Following the removal of most of Topsent's (1928c) species included in *Halicnemia*, leaving only the type species in it, Desqueyroux-Faúndez & Van Soest (1997) subsequently added several other species. They also briefly review the genus and included in it a new species from the Galapagos Is, SE Pacific, and *Higginsia papillosa* Thiele, 1905 (from S Chile). They also noted that several species currently included in *Higginsia* may eventually be transferred to *Halicnemia*. Van Soest (1987b) also remarked on this close similarity, suggesting that the only significant differences relate mainly to reticulate versus radial skeletons in *Higginsia* and *Halicnemia*, respectively. This argument was again raised by Desqueyroux-Faúndez & Van Soest (1997), citing observed similarities between a Galapagos species of *Halicnemia* and other *Higginsia*, as evidence for a close relationship between the genera, and between Desmoxyidae and some poecilosclerids (Raspailiidae, Rhabderemiidae). They suggested that the similarity of the angulated acanthoxeas of both genera was supported by a grade in skeletal architecture halfway between a strictly *Eurypon*-like architecture in *Halicnemia patera* and a strictly reticulate architecture in *Higginsia coralloides*. The Galapagos *Halicnemia* had long styles surrounded by shorter styles and centrotylote oxeas, also observed in *H. patera*, plumose spicule bundles also seen in some *Higginsia* and surface bouquets of special oxeas reminiscent of a raspailiid surface structure. They suggested further that Desmoxyidae and Raspailiidae might be conceivably merged in future revisions – an action not presently contemplated.

Alloscleria Topsent (type species *A. tenuispinosa* Topsent, 1927, by original designation, schizotypes MNHN DT1190) is also referred here to *Halicnemia*, with skeletal structure and spicule geometry similar to the type species but with some differences in its ectosomal skeleton and absence of polytylote oxea megascleres

in *A. tenuispinosa*. This species has long smooth style megascleres (lacking a swollen basal tyle as characteristic of the type species) and two categories of centrotylote acanthoxea microscleres – the smaller being more heavily spined of the two. Its acanthoxeas do not form a prominently erect surface, as in the type species, but are reportedly paratangential and scattered throughout the mesohyl, and its choanosomal skeleton consists of parallel tracts of styles forming a halichondroid skeleton. Given these features it is perplexing why Topsent (1928c) did not associate the genus as having affinities to *Halicnemia* and *Higginsia*.

Quindesmia de Laubenfels, 1950 (type *Hymedesmia inflata* Bowerbank, 1866) is an objective synonym of *Halicnemia*, as its type is a junior synonym of *H. patera* (Rob Van Soest, pers. comm., from re-examination of a slide of the type in the BMNH).

Distribution

North Atlantic (Shetland Islands, Ireland, France, Mediterranean), southeast Pacific (Galapagos Islands, S Chile) and NE Pacific (British Columbia).

HETEROXYA TOPSENT, 1898

Synonymy

Heteroxya Topsent, 1898b: 231; Topsent, 1904b: 133; de Laubenfels, 1936a: 72; Bergquist, 1965: 182.

Type species

Heteroxya corticata Topsent, 1898b (by monotypy).

Definition

Desmoxyidae lacking microscleres but with two sizes of oxea megascleres both with apical spination, the smaller forming a nearly continuous palisade perpendicular to the ectosome and the larger forming both a halichondroid choanosomal skeleton and protruding through the ectosome.

Diagnosis

Thickly encrusting growth form; surface lobate, folded to the contours of the substrate, highly hispid; choanosome with a condensed basal layer of spongin lying on the substrate, without a complete mineral skeletal structure, containing only acanthoxeas distributed without appreciable order on basal spongin and strewn throughout the mesohyl; subectosomal skeleton consists of oxeas or tornotes perpendicular to the ectosome, protruding through the surface, but not embedded in basal spongin; ectosomal skeleton with a perpendicular palisade of smaller acanthoxeas, through which the larger subectosomal oxeas protrude; megascleres curved to sinuous smooth or spined hastate oxeas/tornotes, and curved acanthoxeas; microscleres absent.

Description of type species

Heteroxya corticata Topsent, 1898b (Fig. 4).

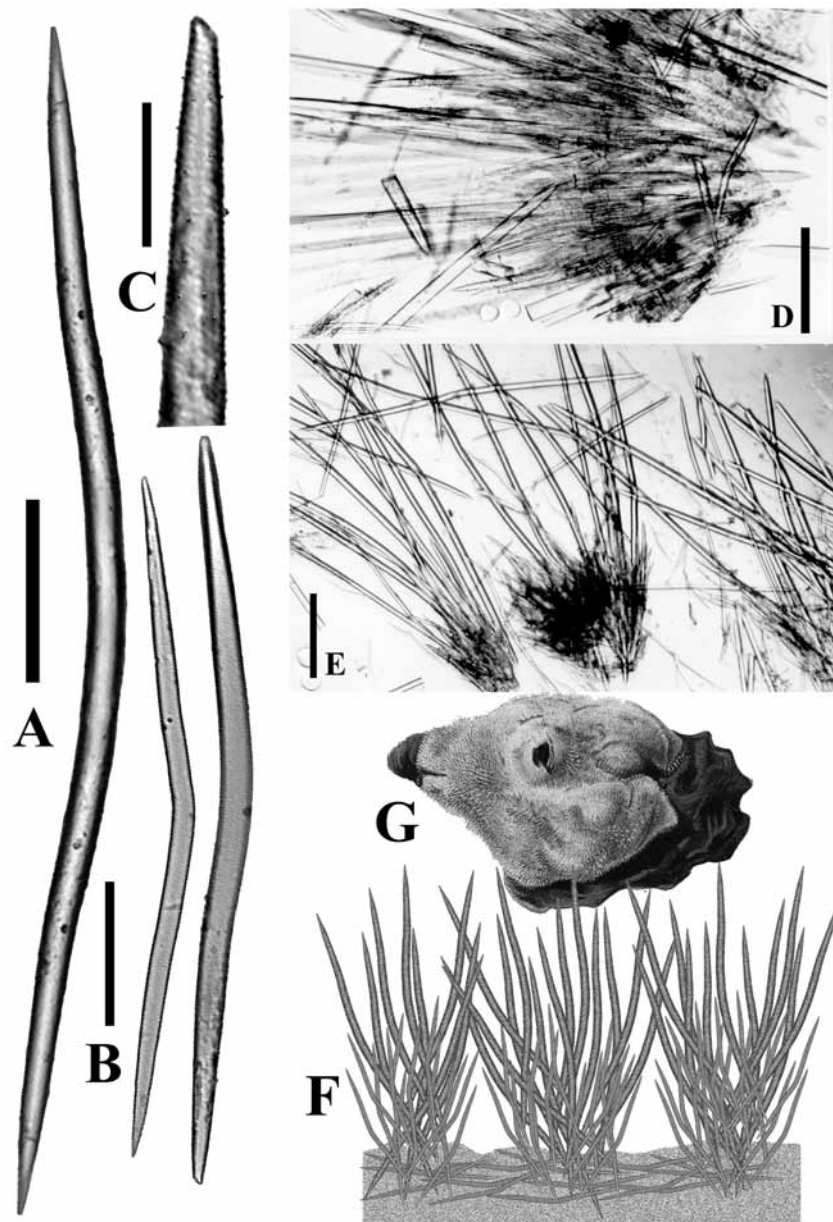


Fig. 4. *Heteroxya corticata* Topsent (slides from holotype). A, larger acanthoxea (scale 250 μm). B, smaller acanthoxeas (scale 50 μm). C, apex of smaller acanthoxea (scale 20 μm). D, enlarged view of cortical ectosomal bundle (scale 100 μm). E, cortical ectosomal bundles (scale 250 μm). F, idealised reconstruction of skeleton. G, holotype (from Topsent, 1904b: pl. 1 fig. 15).

Synonymy. *Heteroxya corticata* Topsent, 1898b: 231; 1904b: 133, pl. 1 fig. 15, pl. 12 figs 22–23.

Material examined. Holotype: MOM (not seen); slide made from holotype – MNHN DT905, BMNH 1930.7.1.46 – Azores, N Atlantic.

Description. Thinly encrusting plaque, hispid surface; choanosome nearly completely lacking skeletal structure, with only acanthoxeas scattered indiscriminantly throughout the mesohyl; cortical ectosome well developed, thick, very spiculose, with two sizes of acanthoxeas, the larger extending into the choanosomal mesohyl interior and protruding a long way through the surface, perpendicular to it, and the smaller forming a nearly continuous perpendicular palisade on or just below the surface; megascleres two sizes of oxeas, both predominantly acanthose, with pronounced central curvature, the larger (1600–2000 \times 20–35 μm) less spined (or sometimes completely

smooth) than the smaller (235–420 \times 12–23 μm), with spination predominantly at apices of spicules; microscleres absent.

Remarks. Topsent (1898b, 1904b, 1928c) remarked on the resemblance between *H. corticata* and *Trachya* (= *Aaptos*, Suberitidae), particularly in surface features, but in other respects their affinities are purely superficial. The higher systematic placement of *Heteroxya* has altered with each successive description in the literature: Aciculida (Topsent, 1898b: 233), Tethyidae (Topsent, 1904b: 134), Axinellida (Topsent, 1928c: 189) and Coelosphaeridae (de Laubenfels, 1936a: 72), but the genus appears to have closest affinities with the Desmoxyidae. Van Soest *et al.* (1990) included *Heteroxya* as a synonym of *Myrmekioderma*, with question, based on Topsent's description of *H. corticata*, but re-examination of the holotype does not indicate such a close relationship as inferred by Topsent. The genus is retained here in Desmoxyidae.

Distribution

N Atlantic.

HIGGINSLIA HIGGIN, 1877**Synonymy**

Higginsia Higgin, 1877: 291; Hallmann, 1917c: 655; Dendy, 1922b: 126; Topsent, 1928c: 39; de Laubenfels, 1936a: 132; Burton, 1959a: 255; Wiedenmayer, 1977b: 156; Hooper & Lévi, 1993b: 1452. *Dendropsis* Ridley and Dendy, 1886: 483, 1887: 191; Hallmann, 1917c: 693; de Laubenfels, 1936a: 132; Lévi, 1973: 606. *Allantella* Hallmann, 1917c: 675. *Desmoxya* Hallmann, 1917c: 649; de Laubenfels, 1936a: 132; Van Soest *et al.*, 1990: 18. Taxonomic decision for synonymy: Hooper & Lévi (1993b) and this work.

Type species

Higginsia coralloides Higgin, 1877 (by subsequent designation, Hallmann, 1917c), (holotype BMNH 1886.12.15.92), possible junior synonym of *Spongia strigilata* Lamarck, 1814: 450 (Wiedenmayer, 1977b) (holotype MNHN DT637).

Definition

Desmoxyidae with sinuous raphidiform ectosomal oxeads/styles protruding through the surface in sparse plumose bundles, supported by long sinuous extra-axial styles in sparse plumose tracts, embedded in a choanosomal skeleton of variable structure (halichondroid to axially compressed) composed of choanosomal oxeads in bundles, with coarsely spined centrangulate microxeads tangential and below the surface (not forming a crust).

Diagnosis

Growth forms erect, lamellate, massive, vasiform or lobate; surface conulose, papillose, often silt covered or membranous. Choanosomal skeleton predominantly with an elaborate system of bundles of megascleres, although skeletal structure ranges from halichondroid with a partially compressed, reticulate axis, and an irregularly plumo-reticulate extra-axial region (*Higginsia*), a compressed axis and a radial, non-plumose extra-axial region (*Dendropsis*), to a lax plumose or plumo-reticulate structure, without axial compression or regional differentiation of the skeleton (*Desmoxya*); spongin fibres usually poorly developed although heavy collagen forms the mesohyl, usually with numerous megascleres and microscleres scattered between main skeletal tracts; all skeletal tracts cored by robust oxeads and/or styles, or sometimes modified further to strongylote megascleres with bifurcated points. Ectosome with a protruding extra-axial skeleton composed of longer oxeads and/or styles, and smaller oxeads/styles forming sparse brushes or tangential layers on the surface. Megascleres oxeads, strongyles and/or styles of 1–3 sizes. Microscleres spined, centrangulate curved or straight microxeads, and sometimes also raphides occurring singly or in bundles (trichodragmata).

Description of type species

Higginsia coralloides Higgin, 1877 (Fig. 5).

Synonymy. *Higginsia coralloides* Higgin, 1877: 291.

Material examined. Holotype: BMNH 1886.12.15.92 – Grenada (Bowerbank slide). Other material. BMNH 1902.10.18.416 – Dendy's specimen RN891.

Description. Erect, lamellate, massive growth form; surface conulose, striated; ectosomal skeleton with slender extra-axial oxeads (occasionally styles) protruding through the surface in sparse plumose bundles, and centrangulate microxeads tangential and below the surface (not forming a crust); extra-axial skeleton with radial tracts of very long, slender, sinuous styles surmounted by the oxeads protruding through the surface, arising from the axis in sparse plumose tracts; choanosomal skeleton halichondroid with a partially compressed, reticulate axis composed of robust oxeads without any obvious fibre component but mesohyl heavily invested with collagen, and abundant centrangulate microxeads scattered throughout; ectosomal oxeads/styles raphidiform, widely curved or sinuous (430–620 × 3–5 µm); extra-axial styles long, slender, sinuous, bases evenly rounded (1100–1650 × 14–22 µm); choanosomal oxeads robust, thick, usually symmetrical, with fusiform points (580–740 × 11–32 µm); microscleres spined, centrangulate, curved or straight microxeads (65–240 × 3–6 µm).

Remarks. The nominal genera *Higginsia*, *Dendropsis* and *Desmoxya* differ essentially in skeletal construction (reticulate or plumo-reticulate; with a compressed axis and radial extra-axis; and plumose-halichondroid, with meandering, occasionally reticulate skeletal tracts, respectively). Most species lack definite axial compression of the skeleton (except *Dendropsis bidentifera* Ridley & Dendy, 1886 (holotype BMNH 1887.5.2.59), the type species, by original designation, of *Dendropsis*), having instead a halichondroid, vaguely reticulate axis, and in most species there is often some differentiation of axial and extra-axial skeletons (except *Desmoxya lunata*), suggesting some sort of affinity with the concept of Axinellida. All three nominal genera share the apomorphy of spined microxeads, but it is not entirely convincing that the major differences in their skeletal structures can be ignored, particularly in the case of *Dendropsis* which has a nearly 'classical axinellid' architecture, in recognising these taxa merely as synonyms of *Higginsia* (e.g., Hallmann, 1917c; Van Soest *et al.*, 1990).

It is possible that resurrection of *Desmoxya* (with type species *Higginsia lunata* Carter, 1885d (by original designation) holotype BMNH 1886.12.15.138) is required to accommodate *Higginsia*-like species that lack any evidence of axial compression (as seen in both *H. lunata* and *H. anfractuosa* Hooper & Lévi, 1993b), having instead a simply halichondroid, meandering reticulation of choanosomal tracts as seen in other axinellid genera such as *Rhaphoxya*. These species also differ from *Higginsia sensu stricto* only in having one size category of megascleres, raphides in addition to spined microxeads, as well as a more lax skeletal architecture. However, intermediate forms of architecture between *Higginsia* and *Desmoxya* are present in some species of *Higginsia* (e.g., *H. massalis*), and this condition is interpreted here as being merely a reduced form of the skeleton that is typical for *Higginsia* (Van Soest *et al.*, 1990). *Allantella* Hallmann (with type species *Trachytedania arborea* Keller, 1889) has spined microstrongyles and is largely synonymous with *Higginsia* (confirmed by examination of specimen ZMB 444 courtesy of R.W.M. Van Soest).

Hallmann (1917c) provided a comprehensive review of the genus and the diagnostic features of species included at that time, although many more species have since been described and all now are in need of detailed revision. Only a few type specimens have yet been located and seen, so it is not possible to undertake

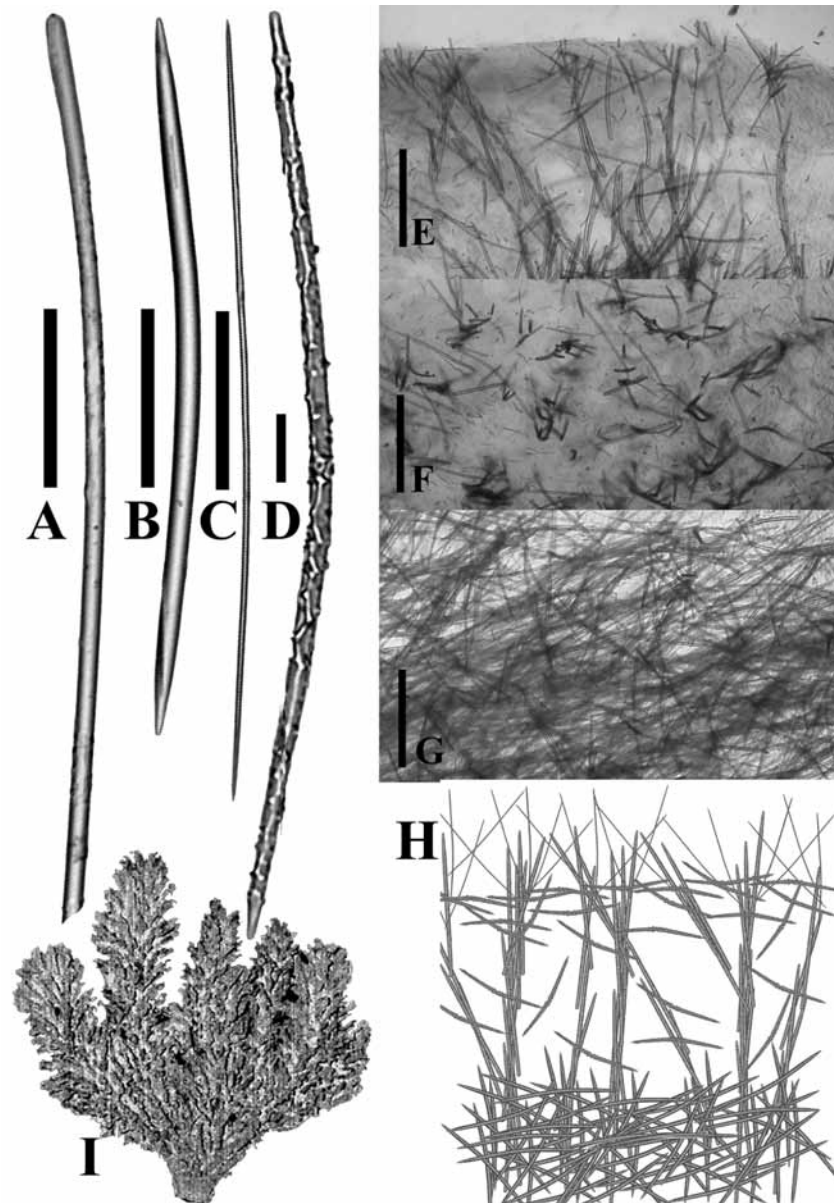


Fig. 5. *Higginsia coralloides* Higgin (holotype and Dendy specimen). A, basal end of extra-axial style (scale 100 μ m). B, choanosomal oxea (scale 100 μ m). C, ectosomal oxea (scale 100 μ m). D, microspined microxea (scale 10 μ m). E, peripheral skeleton (XS) (scale 250 μ m). F, ectosomal skeleton (TS) (scale 250 μ m). G, choanosomal skeleton (scale 250 μ m). H, idealised reconstruction of skeleton. I, holotype of *Spongia strigilata* Lamarck (MNHN DT637), senior synonym of *H. coralloides*.

a review of these species at the present time. Twenty species are thought to be valid: *H. anfractuosa* Hooper & Lévi, 1993b; *H. bidentifera* (Ridley and Dendy); *H. ciccaresei* Pansini & Pesce, 1998; *H. coralloides* Higgin, with varieties *H. c. liberiensis* Higgin, 1877, and *H. c. arcuata* Higgin, 1877 [possible synonym of *H. strigilata* (Lamarck)]; *H. higgini* Dendy, 1922b; *H. lunata* Carter; *H. massalis* Carter, 1885d; *H. mediterranea* Pulitzer-Finali, 1977; *H. mixta* Hentschel, 1912; *H. natalensis* Carter, 1885d; *H. petrosioides* Dendy, 1922b; *H. pumila* (Keller, 1889); *H. robusta* Burton, 1959a; *H. scabra* Whitelegge, 1907; *H. strigilata* (Lamarck); *H. tanekea* Hooper & Lévi, 1993b; *H. tethyoides* Lévi, 1960a; and *H. thielei* Topsent, 1898b (Van Soest, 1987b; Hooper & Lévi, 1993b; Pansini & Pesce, 1998), with *H. papillosa* Thiele, 1905 transferred to *Halicnemia* (Desqueyroux-Faúndez & Van Soest, 1997).

Distribution

Worldwide, but most common in tropical and temperate Indo-Pacific Ocean – Chile, Caribbean, Azores, Ireland, Iceland, Mediterranean, South Africa, West Africa, W Indian Ocean, Seychelles, Red Sea, Gulf of Aden, Indonesia, Palau, SE, NW and NE Australia, New Caledonia.

JULAVIS DE LAUBENFELS, 1936

Synonymy

Julavis de Laubenfels, 1936a: 79; Van Soest & Lehnert, 1997: 502.

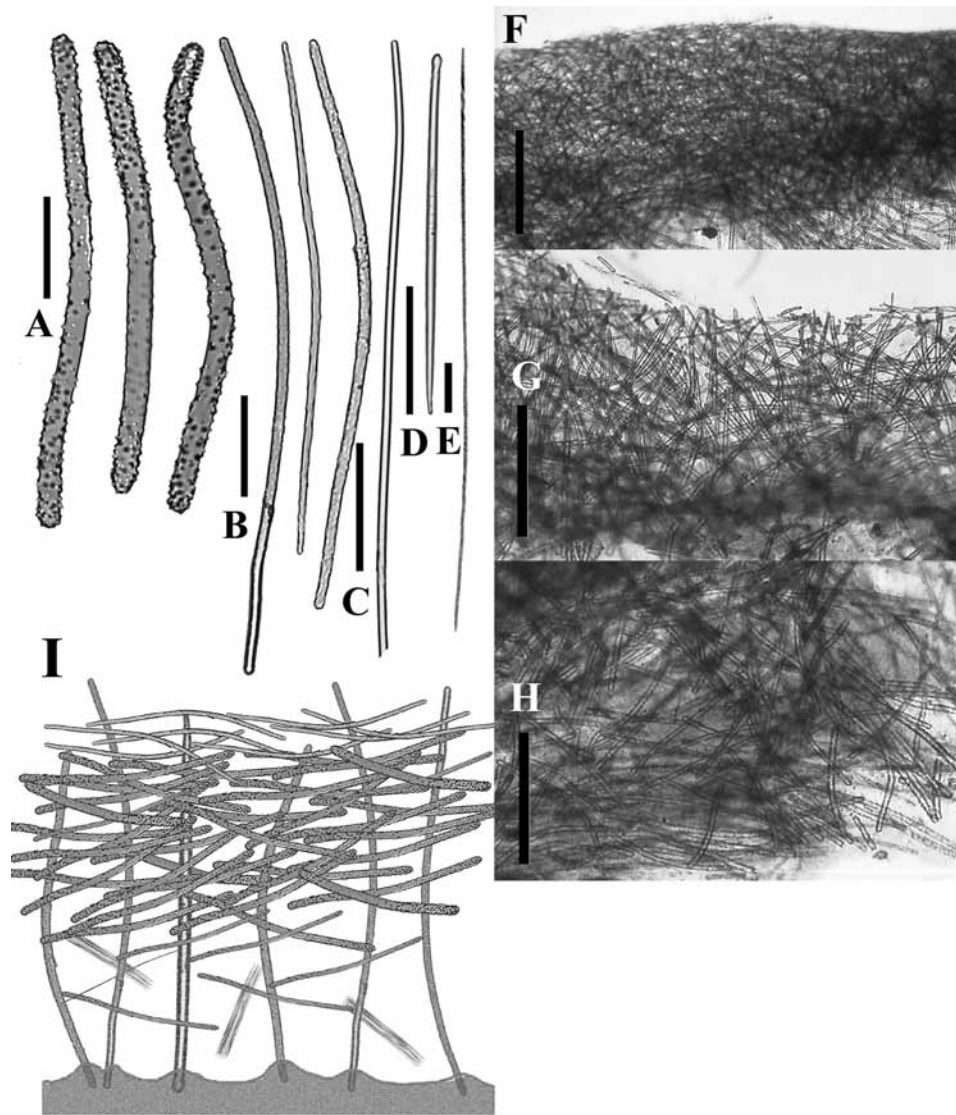


Fig. 6. *Julavis levis* (Kirkpatrick) (holotype). A, choanosomal acanthostrongyles (scale 50 μm). B, ectosomal acanthostrongyles (scale 50 μm). C, basal end of smooth strongyle (scale 100 μm). D, smooth style (scale 100 μm). E, raphide (scale 10 μm). F, peripheral skeleton (XS) (scale 250 μm). G, peripheral skeleton (XS) (scale 100 μm). H, choanosomal skeleton (scale 100 μm). I, idealised reconstruction of skeleton.

Type species

Tedania levis Kirkpatrick, 1900b (by original designation).

Definition

Desmoxyidae with spiny strongyles forming a tangential ectosomal skeleton and raphides in dragmata.

Diagnosis

Thinly encrusting growth form; choanosomal skeleton reduced, consisting of a halichondroid-reticulate arrangement of acanthose strongyles forming a basal skeleton, and longer smooth strongyles and styles oriented perpendicularly to the surface, single or in bundles; ectosomal skeleton with smaller spined strongyles lying tangential to the surface; megascleres are long, thick, curved or vermiform acanthose strongyles, and longer smooth strongyles/styles; microscleres are raphides in trichodragmata.

Description of type species

Julavis levis (Kirkpatrick, 1900b) (Fig. 6).

Synonymy. *Tedania levis* Kirkpatrick, 1900b: 355, pl. 14, fig. 4.

Material examined. Holotype: BMNH 1900.10.19.16 – Funafuti (Ellice Islands) (=Tuvalu), central S Pacific.

Description. Thinly encrusting on dead coral, with smooth surface; ectosomal skeleton a tangential, criss-cross layer of thinner, curved, smooth, granular or vestigially microspined strongyles; choanosomal skeleton halichondroid reticulate, composed of loose tracts of larger, curved or sinuous, occasionally vermiform, prominently acanthose strongyles with poorly developed spongin fibres but abundant granular collagen dispersed throughout the mesohyl; skeletal reticulation denser near the periphery than towards the basal skeleton, with some peripheral tracts forming distinct spicule bundles; few larger, smooth strongyles and styles ascend to the surface from the basal skeleton to the periphery in more-or-less plumose or radial tracts or as single spicules; megascleres

acanthose strongyles of 2 sizes, both curved, sinuous or sometimes vermiform, the smaller with vestigial spination, the larger prominently spined (250–300 × 3–12 µm), and long smooth, curved or sinuous strongyles or styles (245–1380 × 4–12 µm); microscleres raphides in trichodragmata (150–200 × 6–12 µm).

Remarks. De Laubenfels (1936a) erected *Julavis* for Kirkpatrick's (1900b) species, based on a single encrusting specimen containing two distinct categories of spiny strongyles and raphide microscleres. De Laubenfels overlooked the presence of the longer smooth strongyles and styles that arise from the basal skeleton, although admittedly these are uncommon in the holotype slide preparation (BMNH 1900.10.19.16a), and also mentioned by Kirkpatrick in the original description. Kirkpatrick initially assigned his species to *Tedania* based on the possession of raphide microscleres as well as diactinal ectosomal megascleres but these characters are not truly homologous to the onychaetes and ectosomal tyloles of *Tedania*; moreover *T. levis* contains spined diactinal choanosomal megascleres and differentiated axial and extra-axial spicules. De Laubenfels subsequently erected the genus *Julavis* to his admittedly 'unsatisfactory family' Acarniidae (=Microcionidae in the contemporary sense) based on possession of spiny spicules (megascleres), but the genus appears to have closest resemblance to the Desmoxyidae having a halichondroid reticulate choanosomal skeleton and more organised tangential ectosomal skeleton, including spined diactinal spicules and raphide microscleres. The genus contains only two species so far, and still relatively poorly known, although the recent description of a new species and redescription of the type species by Van Soest & Lehnert (1997) has made the genus now perfectly recognisable.

Distribution

Tuvalu, central Pacific, and Jamaica, Caribbean.

MICROXISTYLA TOPSENT, 1928

Synonymy

Microxistyla Topsent, 1928c: 179.

Type species

Microxistyla petrina Topsent, 1928c (by monotypy).

Definition

Desmoxyidae with plumose bundles of smooth centrangulate or straight microxeas forming a nearly continuous palisade on the surface, supported by plumose extra-fibre tracts of choanosomal styles and a halichondroid reticulation of the same styles below.

Diagnosis

Encrusting-massive growth form, stony texture; ectosomal skeleton with erect, plumose bundles of smooth microxeas forming a nearly continuous palisade on the surface; extra-axial region cavernous with plumose tracts of choanosomal styles; choanosomal skeleton a confused halichondroid reticulation of smooth robust styles without fibres but bonded together with minimal collagen; microscleres smooth straight or centrangulate microxeas.

Description of type species

Microxistyla petrina Topsent, 1928c (Fig. 7).

Synonymy. *Microxistyla petrina* Topsent, 1928c: 179, pl. 6 fig. 18.

Material examined. Holotype: MOM (not seen), schizotypes MNHN DT1141, BMNH 1930.7.1.42 – Cape Verde Is, NE Atlantic.

Description. Encrusting-massive, irregular surface perforated by small oscula, stony consistency; ectosomal skeleton with erect, plumose bundles of microxeas arising from subectosomal tracts forming a nearly continuous palisade on the surface; subectosomal skeleton plumose, cavernous, with multispicular bundles of styles; choanosomal skeleton riddled with aquiferous canals, between which is an irregularly halichondroid reticulate skeleton composed of robust styles poorly bound with sparse collagen; megascleres curved thick styles (400–575 × 20–30 µm); microscleres smooth centrangulate or straight microxeas (60–160 × 2–4 µm).

Remarks. Topsent (1928c) remarked that this monotypic genus showed affinities with the genera *Axinyssa* (Halichondriidae) and *Ceratopsion* (Raspailiidae) in having oxoete microscleres, but this similarity is probably superficial given that microxeas found in either of these genera are not centrangulate. Similarly, in texture and skeletal architecture Topsent (1928c) suggests that *M. petrina* shows similarities to the stony haplosclerids (*Petrosia*, *Strongylophora*), emphasized by the paucity of spongin fibres or collagen within the choanosome, but this is again only superficial. The genus is more obviously related to the desmoxyids (*Higginsia*, *Desmoxya*) with centrotlyote microscleres, and with similarities to some halichondriids (like *Spongosorites dendyi* (Topsent) and *S. placenta* (Topsent), which have centrotlyote modifications to some spicules (although in the Halichondriidae these are classed as megascleres and not microscleres as in Desmoxyidae). Topsent omitted to mention that the species has a specialised ectosomal skeleton in which plumose bundles of microxeas project from peripheral subectosomal tracts. However, the holotype is dry and this may have become detached in his material.

Distribution

Monotypic, known only from the NE Atlantic and Sea of Okhotsk.

MYRMEKIODERMA EHLERS, 1870

Synonymy

Myrmekioderma Ehlers, 1870: 28; Bergquist, 1965: 177. *Acanthoxifer* Dendy, 1905: 156; Dendy, 1922b:129; Bergquist, 1965: 177. *Anacanthaea* Row, 1911: 329; Van Soest *et al.*, 1990: 31. *Callites* Schmidt, 1868: 16; Van Soest *et al.*, 1990: 31. *Neoprosypa* de Laubenfels, 1954: 189. Taxonomic decision for synonymy. Van Soest *et al.* (1990: 31).

Type species

Alcyonium granulatum Esper, 1830 (by monotypy).

Definition

Desmoxyidae with a detachable ectosomal skeleton consisting of smaller (acanth-)oxeas in brushes perpendicular or paratangential

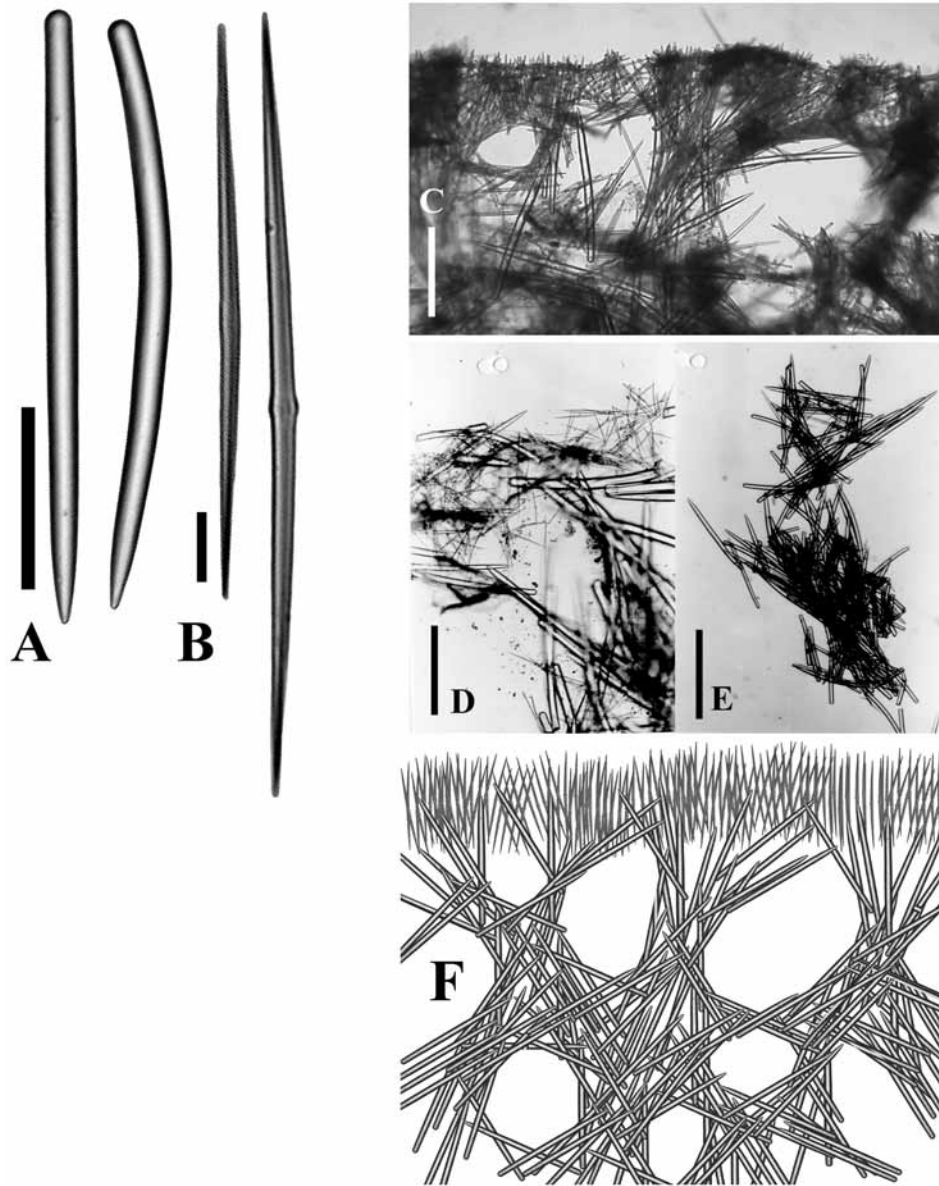


Fig. 7. *Microxistyla petrina* Topsent (schizotypes). A, styles (scale 150 μm). B, microxeas (scale 10 μm). C, peripheral skeleton (scale 250 μm). D, ectosomal peel (scale 200 μm). E, choanosomal spicule tract (scale 400 μm). F, idealised reconstruction of skeleton.

to the surface, supported by larger choanosomal (acanth-)oxeas, strongyles or styles forming a slightly compressed halichondroid reticulation in the central portion of the choanosome and a more cavernous peripheral skeleton of oblique spicule tracts, with wispy trichodragmata of raphides in one or two size classes dispersed throughout the skeleton.

Diagnosis

Massive or encrusting growth forms. Surface hispid, with characteristic excavating meandering, sinuous or straight canals and grooves sometimes forming polygonal tuberculate plates. Choanosomal skeleton collagenous, with compressed central portion composed of a confused halichondroid mass of larger choanosomal megascleres ranging from acanthoxeas and oxeas, strongyles or less frequently styles, forming irregular, ascending, multispicular tracts bound together with sparse collagen (spongin fibres present in some

species but not all). Subectosomal skeleton composed of ascending tracts of the same spicules running radially or obliquely to the surface, with larger choanosomal megascleres protruding, and frequently cavernous towards the periphery. Ectosomal skeleton without specialised spiculation although smaller (acanth-)oxeas protrude from the subectosomal region, forming a dense 'peel' of closely adjacent brushes perpendicular or paratangential. Megascleres consist of two distinct categories of oxeas, strongyles, or more rarely styles, sometimes sinuous and centrally flexed, either entirely smooth or with even spination, the larger choanosomal spicules more variable in their terminations than the smaller ectosomal spicules which are typically oxeas or acanthoxeas. Microscleres raphides in trichodragmata, in one or more categories, the larger usually sinuous or curved.

Description of type species

Myrmekioderma granulata (Esper, 1830) (Fig. 8).

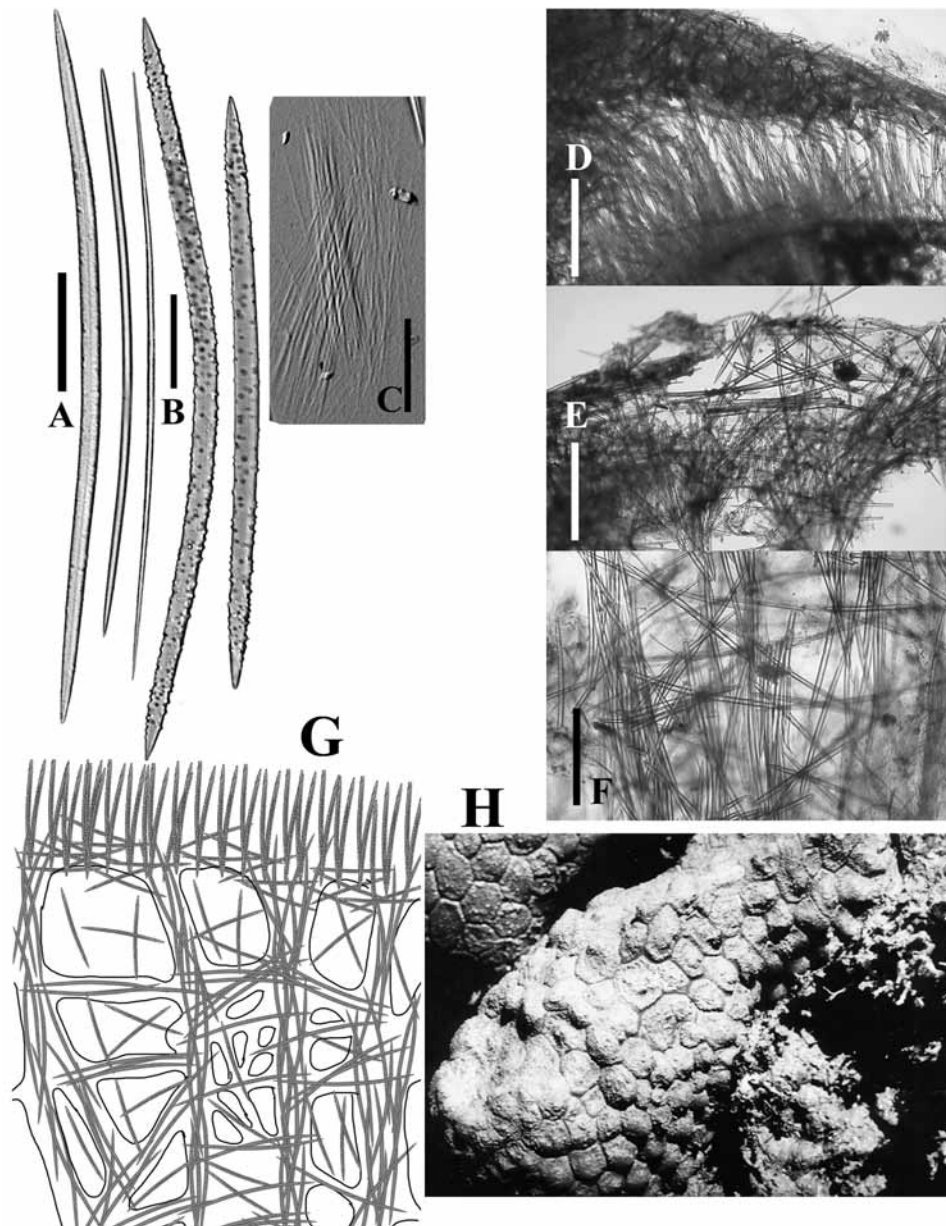


Fig. 8. *Myrmekioderma granulata* (Esper) (specimen QMG303135). A, choanosomal oxeas (smooth or vestigial spination) (scale 100 μm). B, ectosomal acanthoxeas (scale 50 μm). C, trichodragmata (scale 50 μm). D, peripheral skeleton (scale 250 μm). E, subectosomal skeleton (scale 250 μm). F, choanosomal skeleton (scale 250 μm). G, idealised reconstruction of skeleton. H, specimen in situ (photo author).

Synonymy. *Alcyonium granulatum* Esper, 1830: 71; *Myrmekioderma granulata*; Ehlers, 1870: 28. *Acanthoxifer ceylonensis* Dendy, 1905: 157. *Myrmekioderma tylota* de Laubenfels, 1954: 119. *Neoprosopa atina* de Laubenfels, 1954: 190. *Acanthoxifer fourmanoiri* Lévi, 1956c: 5.

Material examined. Holotype: Unknown – Indonesia. Other material. Numerous specimens, widespread tropical Australasia (see Hooper & Lévi, 1993b: 1449; Hooper *et al.*, 1997: 8). Holotypes of junior synonyms (see below).

Description. Massive, bulbous, partially burrowing, light orange-brown to bright orange exterior; surface convoluted with large conules or rounded or polygonal plates, each separated by shallow but distinct grooves, excavated channels containing large oscula; ectosomal skeleton a detachable ‘peel’, with a distinct crust

of smaller ectosomal (acanth-)oxeas arising from the subectosomal region ($305\text{--}708 \times 3\text{--}12 \mu\text{m}$) forming a continuous paratangential palisade, supported below by long, pillar-like tracts of larger choanosomal (acanth-)oxeas and styles producing a cavernous subdermal region; choanosome cavernous, with a vaguely halichondroid reticulate skeletal structure, sometimes with a compressed central portion, and with differentiated primary and secondary spongin fibres and spicule tracts; primary, ascending, fibres very large, with up to 50 spicules per tract but diminishing in size towards the periphery, more-or-less regularly spaced, interconnected by secondary, transverse or oblique, pauci-, uni- or aspicular fibres; fibres cored by larger choanosomal (acanth-)oxeas ($495\text{--}950 \times 8\text{--}22 \mu\text{m}$). Two categories of megascleres differing only in size and distribution within skeleton, both straight or slightly curved

at centre, rarely asymmetrical, with variable terminations, usually tapering to sharp fusiform points but also with telescoped, strongylote, styloid modifications and other terminal deformities, and both categories of spicules may be entirely smooth or lightly and evenly acanthose; ectosomal spicules tend to be mostly oxeas whereas choanosomal megascleres have greater geometric variability. Microscleres raphides mostly in trichodragmata (110–155 × 10–15 µm).

Remarks. Bergquist (1965) meticulously redescribed the type species of *Myrmekioderma* from a number of specimens from a range of geographic localities. She showed conclusively that the type species of *Acanthoxifer* (*A. ceylonensis* Dendy, 1905 (by monotypy) holotype BMNH 1907.2.1.54,55) and *Neoprosypa* (*N. atina* de Laubenfels, 1954 (by monotypy) holotype USNM 22974) were conspecific and also identical to *M. granulata*. Bergquist also noted that *M. granulata* had a wide geographical distribution with a corresponding high degree of skeletal variability, particularly in the presence, absence and size of certain spicule categories, and the presence or absence of spination on megascleres.

Bergquist (1965: 182) also discussed at length the relationships between *Myrmekioderma*, *Acanthoxifer*, *Anacantha* (type species *A. nivea* Row, 1911 (by monotypy) holotype BMNH 1912.2.1.54), *Spongosorites* and *Heteroxya*, and she concluded that *Myrmekioderma*, *Anacantha* and *Heteroxya* were good genera, and most closely related to *Higginsia*. Conversely, Van Soest *et al.* (1990) included *Anacantha* in synonymy with *Myrmekioderma*. Two species were initially assigned to *Anacantha*, the type species and *A. rea* de Laubenfels (1934: 11). Apart from megasclere size and live colouration both species are identical. In external morphology, distribution of pores and ornamentation of pore grooves *A. nivea* and *A. rea* are also very similar to *Myrmekioderma granulata* (Esper), which by contrast is bright orange whereas the two *Anacantha* species are white and dark pinkish-grey, respectively. In addition, *M. granulata* has acanthose microxeas, choanosomal oxeas, and a separate category of ectosomal oxeas, whereas *Anacantha* has only oxeas. However, several regional populations of *M. granulata* have their spiculation reduced to only smooth oxeas, in addition to microxeas (e.g., Hooper *et al.*, 1997), and in this regard *Anacantha* fits comfortably within *Myrmekioderma*. Van Soest *et al.* (1990) commented further on the generic synonymy of *Myrmekioderma*, and included *Callites* (type species *C. lacazii* Schmidt, 1868 (by monotypy) fragment of holotype BMNH 1868.3.2.3) into this synonymy.

Subsequent to Bergquist's (1965) work the genus has been closely examined by Van Soest *et al.* (1990: 31), Diaz *et al.* (1991), Hooper & Lévi (1993b: 1448) and Hooper *et al.* (1997: 6). Together these studies demonstrate that *Myrmekioderma*, *Didiscus* and *Higginsia* are closely related and most appropriately assigned to the same family. *Myrmekioderma* and *Didiscus* are superficially very similar and both easily recognisable in the field by their deeply sculptured sinuous and plate-like grooves on the surface, having an ectosome composed of smaller spicules forming an erect palisade over tangential larger spicules, and a similar basic choanosomal skeletal organisation (Van Soest *et al.*, 1990; Diaz *et al.*, 1991). *Myrmekioderma* lacks discorhabd microscleres, characteristic of *Didiscus*, but has instead bundles of sinuous raphides (trichodragmata). The genus has been traditionally defined with lightly acanthose ectosomal oxeas (e.g., Bergquist, 1965; Hooper & Lévi, 1993b), but Diaz *et al.* (1991) correctly note that these ectosomal spicules are as frequently smooth as they are acanthose, and they emend the definition accordingly. Hooper & Lévi (1993b)

retained this genus in the family Desmoxyidae, supporting their decision with chemotaxonomic evidence based on an inferred close relationship between *Higginsia* and *Myrmekioderma* (Hooper *et al.*, 1992). However, morphological support for homology between the occasionally acanthose ectosomal oxeas in *Myrmekioderma* and the true ectosomal acanthoxeas in *Higginsia* is still equivocal, with the consequence that Hooper *et al.* (1997) returned it to Halichondriidae. The overall similarity between the ectosomal structure, choanosomal organisation and spicule composition (apart from the possession of microxeas or discorhabds, respectively) largely supports the inferred close relationship between *Myrmekioderma* and *Didiscus*, of which the latter had been previously included in Halichondriidae (e.g., Van Soest *et al.*, 1990). Conversely, structural similarities in the erect palisade of ectosomal spicules is remarkable between *Myrmekioderma* and *Higginsia* (see illustrations in Hooper & Lévi, 1993b). As a consequence of these discrepancies both *Myrmekioderma* and *Didiscus* are now referred to the Desmoxyidae, to acknowledge their closer affinities to genera such as *Higginsia*. This decision is supported by the findings of Van Soest & Lehnert (1997) who recently redescribed and revived the genus *Julavis*, previously *incertae sedis*. They showed that *Julavis* had obvious morphological links with *Myrmekioderma* (with wispy trichodragmata) and *Higginsia* (coarsely spined diactinal spicules), and on this basis they re-assigned all these genera to Desmoxyidae.

Van Soest *et al.* (1990) included six species in *Myrmekioderma*, of which only two live in the Indo-west Pacific, and a seventh species should also be included: *M. dendyi* (Burton, 1959a) from the south Arabian coast and Indonesia; *M. granulata* widespread throughout the Indo-west Pacific; *M. nivea* (Row, 1911) from the Red Sea; *M. rea* de Laubenfels, 1934 from the vicinity of Puerto Rico; *M. spelaea* (Pulitzer-Finali, 1983) from the Mediterranean; *M. styx* de Laubenfels, 1953a from the Gulf of Mexico; and *M. tulearensis* (Vacelet *et al.*, 1976) from SW Madagascar.

Distribution

Widely distributed in shallow tropical and subtropical oceans throughout the Indo-west Pacific: Mediterranean, Madagascar, Aldabra, Seychelles, Gulf of Manar, Indonesia, NW Australia, northern Great Barrier Reef, central western Pacific – Ponape, Truk, Ebon Atoll, Palau, Ifaluk, Chesterfield Islands, New Caledonia.

NEGOMBO DENDY, 1905

Synonymy

Negombo Dendy, 1905: 127. *Oxylatrunculia* Hoshino, 1981: 221.

Type species

Negombo tenuistellata Dendy, 1905 (by monotypy).

Definition

Desmoxyidae with a halichondroid skeleton of styles and/or oxeas and with sanidaster-like acanthose microrhabds.

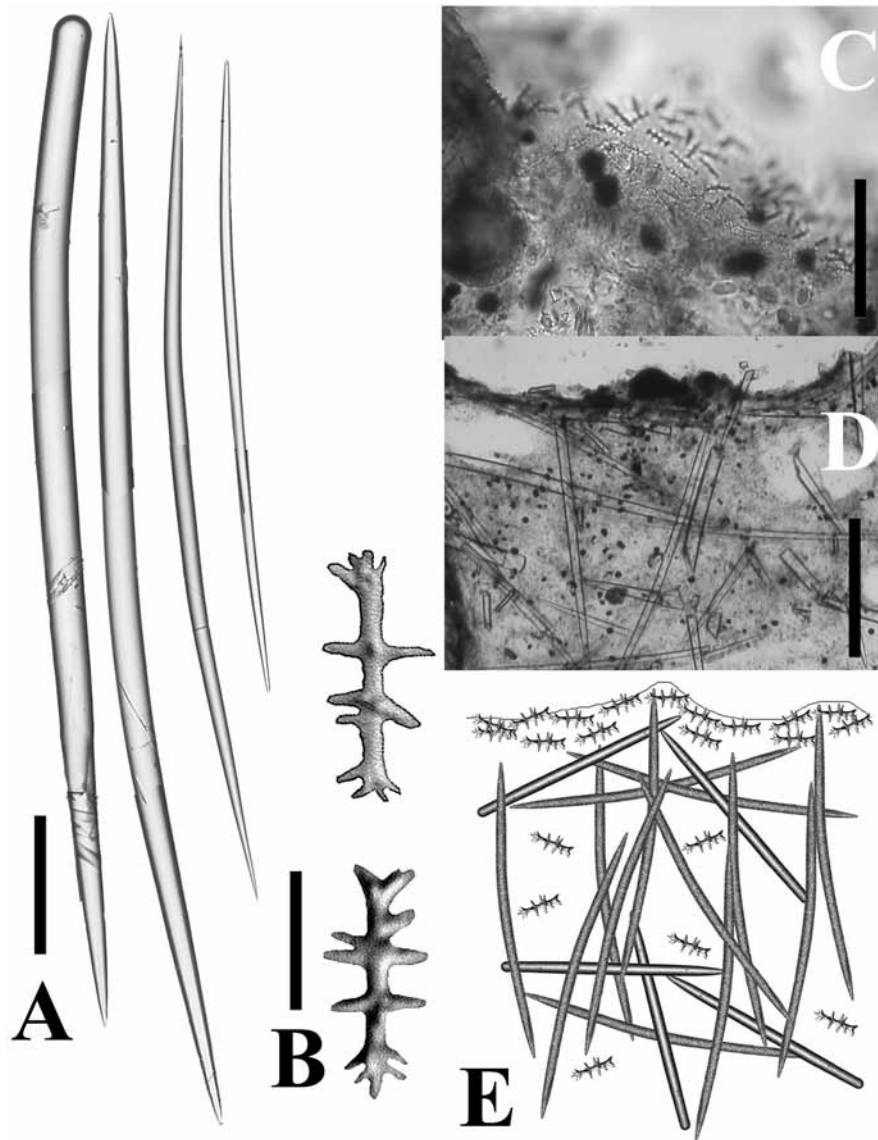


Fig. 9. *Negombo kellyae* sp. nov. (holotype OCDN3701-I). A, choanosomal oxeas and styles (scale 300 μ m). B, acanthose sanidaster-like microrhabds (scale 10 μ m). C, peripheral skeleton illustrating disposition of microrhabds on surface (scale 100 μ m). D, halichondroid choanosomal skeleton (scale 500 μ m). E, idealised reconstruction of skeleton.

Diagnosis

Massive fistular, with a tangential surface layer of sanidaster-like acanthose microrhabds which are also scattered within the mesohyl lining the canals. Choanosomal skeleton with halichondroid tracts of large styles and/or oxeas forming longitudinal or radial, compact tracts.

Description of type species

Negombo tenuistellata Dendy, 1905.

Synonymy. *Negombo tenuistellata* Dendy, 1905: 127–128, pl. 5, fig. 8.

Material examined. Holotype (not seen): BMNH 1907.2.1.28 – Sri Lanka. Comparative material. Holotype of *Negombo kellyae* sp. nov.: BMNH 2000.9.15.1 (OCDN3701-I) – Pemba I., W Tanzania, 5°0.60'S, 39°40.14'E, coll. CRRF, 26.i.96.

Description of type species (from Dendy, 1905). Sponge massive with fistular outgrowths. Surface roughened with foreign

inclusions, hard and slightly incompressible. Oscula and pores not observed. Texture soft and flexible. Ectosomal skeleton with a layer of sanidasters lying tangentially or irregularly scattered on the surface, together with abundant foreign debris. Choanosomal skeleton with very large gently curved styles and oxeas forming confused longitudinal halichondroid tracts, apparently without spongin fibres, and with sanidasters lining the aquiferous system. Megascleres are smooth styles and oxeas 540–1100 \times 12–17 μ m. Microscleres are acanthose microrhabds (sanidasters) with irregular whorls of spines along the shaft, 12–15 μ m in length.

Description of *Negombo kellyae* sp. nov. (Fig. 9). Massive lump, slightly hemispherical. Texture firm, spiculose, sticky, tears, encrusted by other sponges and detritus. Large central oscule. Black alive, with 'sweet, pleasing' odour. Ectosome heavily encrusted with coral debris, diatoms, and foreign spicules, with thin tangential or paratangential layer of sanidasters 2–5 deep forming sparse crust on the surface. Choanosome with a sparse halichondroid reticulate skeleton composed of large oxeas and styles, the latter less common than the former, in two intergrading

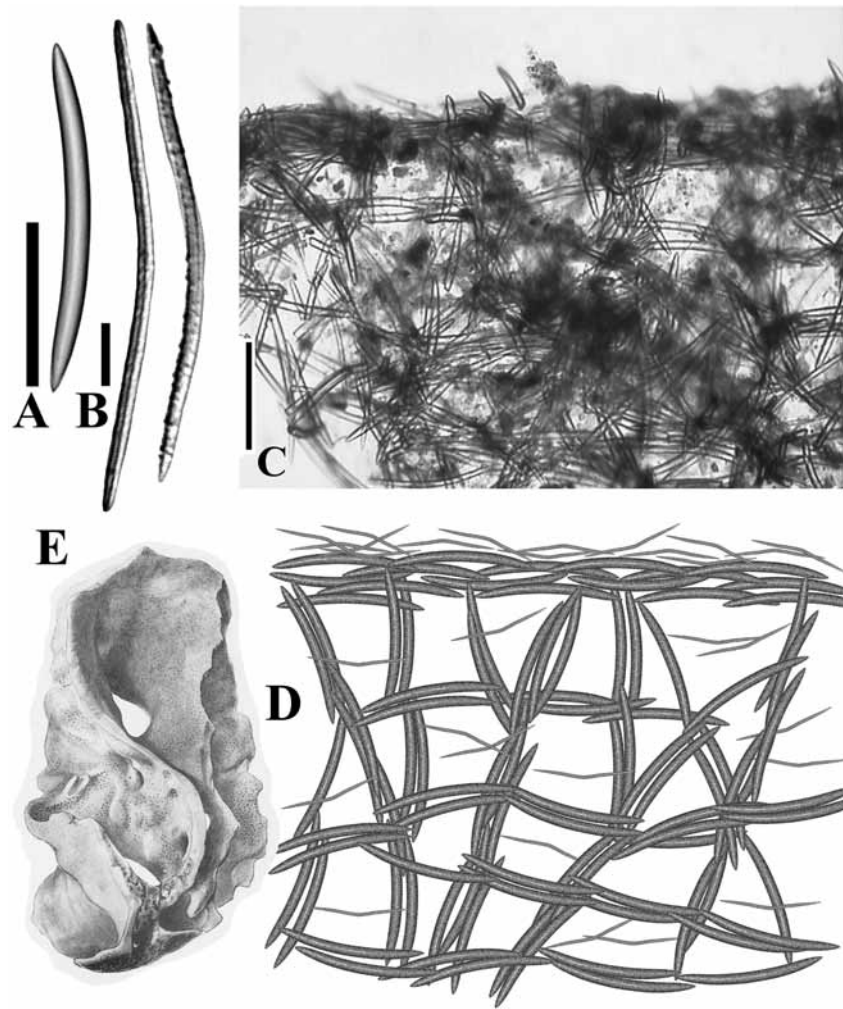


Fig. 10. *Parahigginsia phakellioides* Dendy (holotype). A, oxea (scale 150 μm). B, microxeas (scale 10 μm). C, peripheral skeleton (scale 1 mm). D, idealised reconstruction of skeleton. E, holotype (from Dendy, 1924: pl. 11, fig. 4).

size classes. Reticulation open-meshed, with meshes up to 500 μm wide, bounded by uni- or paucispicular tracts. No spongin fibres observed. Spicule tracts near the surface slightly diverging, paucispicular, not protruding through the surface. Mesohyl heavily collagenous containing abundant cyanobacteria. Choanocyte chambers lined by sparse sanidasters, fewer than at the surface. Few interstitial spicules present. Megascleres oxeas and styles with approximately the same geometry, very long and robust, slightly curved at the centre, long tapering points (1325–(1814)–2240 \times 37–(51)–66 μm). Smaller oxeas similar in shape but much less robust (765–(922)–1245 \times 22–(27)–34 μm). Microscleres acanthose microrhabds resembling sanidasters, 18–26 μm long, with large spines (up to 3 μm long) scattered over shaft, not in whirls and not discoid in shape. *Etymology.* Named for Michelle Kelly for discovering this species.

Remarks. Hooper (1986) and Wiedenmayer (1989) regarded *Negombo tenuistellata* as a synonym of *Latrunculia*, while de Laubenfels (1936a) considered the possibility that *Negombata* was synonymous with *Negombo*. Examination of *Negombo tenuistellata* Dendy by Kelly-Borges & Vacelet (1995) upheld the generic status of *Negombo* and concluded that it was distinct from *Latrunculia*, *Diacarnus* and *Negombata* based on differences in skeletal structure, gross morphology and spiculation. The large oxea and styloid megascleres, the halichondroid skeletal architecture and the geometry of

microrhabds suggest that the genus might be best assigned to Desmoxyidae, closest to *Didiscus*. Microrhabds in *Negombo* and *Didiscus* appear to be modified microxeas, whereas those of *Latrunculia* (acanthodiscorhabds), and *Diacarnus* and *Negombata* (spinorhabds) have different geometry and are not considered to be homologous (M. Kelly, pers. comm.) (see chapters on Podospongiidae and Latrunculiidae in this work).

Oxylatrunculia Hoshino, 1981 (type species *Oxylatrunculia acanthosanidastra* Hoshino, 1981) is virtually identical to *N. tenuistellata* but having a more radiate skeletal architecture, much larger spiculation with exclusively oxecote megascleres. It too clearly belongs to *Negombo* making *Oxylatrunculia* a junior synonym.

The genus presently contains three species: *Negombo tenuistellata* Dendy, *N. acanthosanidastra* (Hoshino) and *N. kellyae* sp.nov. described here. The new species differs from *N. tenuistellata* in having much larger megascleres and microscleres, having predominantly oxeas in the skeleton (whereas the type species has predominant styles), having a much more lax and sparse choanosomal reticulation (the type species has long wispy halichondroid tracts), and in its live specimen characteristics (the type species is fistulose, tubular, yellowish grey). In spicule dimensions the present species is more similar to *N. acanthosanidastra* but megascleres consist of both oxeas and styles (only oxeas in the Japanese species), sanidasters

have several large spines but is not microspined (unlike the latter), and live characteristics (massive, sepia coloured).

Distribution

Japan, Sri Lanka, Tanzania.

PARAHIGGINSIA DENDY, 1924

Synonymy

Parahigginsia Dendy, 1924: 375; de Laubenfels, 1936a: 159; Bergquist, 1970: 22.

Type species

Parahigginsia phakellioides Dendy, 1924 (by monotypy).

Definition

Desmoxyidae with a glabrous ectosomal skeleton containing only curved acanthose microxeas lying tangentially, supported below by a dense peripheral crust of smooth choanosomal oxeas becoming isotropic and more compressed towards the axis.

Diagnosis

Erect, lamellate, lobate growth forms; surface smooth, not hispid; ectosome glabrous, containing only spongin and scattered acanthoaxoas lying tangential to the surface; extra-axial skeleton not clearly delineated from axis, but consisting of irregularly anastomosing and ascending primary and secondary tracts of choanosomal oxeas, which do not protrude through the surface but become more ordered and compact near the periphery, forming a dense crust below the ectosome; choanosomal skeleton with a condensed axial reticulation of oxeas forming irregular isotropic tracts,

without distinct fibres or obvious collagenous spongin; megascleres smooth oxeas of a single category; microscleres curved acanthose microxeas.

Description of type species

Parahigginsia phakellioides Dendy, 1924 (Fig. 10).

Synonymy. *Parahigginsia phakellioides* Dendy, 1924: 375, pl. 11 fig. 4, pl. 15 figs 32–33.

Material examined. Holotype: BMNH 1923.10.1.156 – North Cape, New Zealand.

Description. Branching and anastomosing, curved, thinly lamellate growth form; surface smooth, regular, with distinct osculiferous inhalant and porous exhalant surfaces; texture hard, brittle; ectosomal skeleton with membranous skin-like surface bearing scattered tangential microxea microscleres on the surface, multispicular tracts of choanosomal oxea megascleres forming the dense tangential crust just below the surface, up to 5 spicules thick; ascending choanosomal spicule tracts do not protrude through the surface; choanosomal skeleton a dense petrosiid-like isotropic reticulation of robust oxeas forming thick irregular tracts, 2–8 spicules thick, without spongin fibres but bound together with sparse collagen, and with large oval meshes up to 500 µm diameter; microxea microscleres also scattered within the mesohyl; megascleres short, stout, slightly curved hastate oxeas or sometimes strongly oxeas (280–355 × 18–23 µm); microscleres slightly curved, minutely spined microxeas with evenly dispersed spines (78–95 × 1–2 µm).

Remarks. *Parahigginsia* is closely related to *Higginsia* in skeletal construction and spiculation, differing only by its *Phakellia*-like lamellate growth form, smooth ectosome, and absence of long slender megascleres forming the extra-axial skeleton.

Distribution

Monotypic, known only from New Zealand.